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DWARFISM IN A SABELLID POLYCHAETE, A STUDY OF AN INTERSTITIAL SPECIES

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Sabellid polychaetes are tubicolous worms that feed by means of a crown of tentacles ordinarily extending from the distal end of a mud-encrusted, parchment or mucous tube. The numerous species together exhibit a remarkable range in size, from relatively giant forms such as *Eudistylia vancouveri* (up to 30 cm long and a centimeter wide) to semi-microscopic species barely visible to the naked eye. The present account is of a species of the subfamily Fabricinae, so small as to be truly microscopic, which has an interstitial detrital habitat. Its interest is that the species apparently represents the ultimate degree of dwarfism possible, and that since live individuals are virtually transparent, they elegantly display their internal structure and activity. Previous accounts of internal structure have been based on dissected and sectioned specimens of larger kinds (Nicol, 1930).

Material and Methods

The material studied was found in detritus accumulating along the shaded sides of wood floats in a small protected lagoon of Coconut Island in Kaneohe Bay, Oahu, Hawaii. Specimens were found only by means of a low-power microscope and by virtue of their characteristic thrashing movements when disturbed. The species may have a wide distribution but without such movement individuals are not likely to be seen, the local agitation of detritus particles being the most obvious sign of their presence. The overall length of a mature individual, including tentacles, is about 2.5 mm maximum. Body length exclusive of tentacles is about 1.8 mm. Juveniles of much smaller size are usually present.

Results

Structure and function

The organization and activities of this small sabellid are basically the same as in the largest. They relate primarily to feeding by means of the tentacular crown when protruded from the anterior end of the tube, to the formation of the tube itself, and to behavior within the tube. Inasmuch as individuals abandon the tube upon any disturbance, the subsequent explorative activity is also important in this species. The three main divisions of the worm are the head (tentacle and collar region), the thorax, and the abdomen (Fig. 1A).

When at rest, the worm lies with the prostomial crown of tentacles extending entirely beyond the distal end of the tube. The crown consists of a distinct right and left unit, each consisting of three radioles bearing seven or eight pairs of long lateral filaments, or pinnules, which extend to the crown perimeter (Fig. 1B).

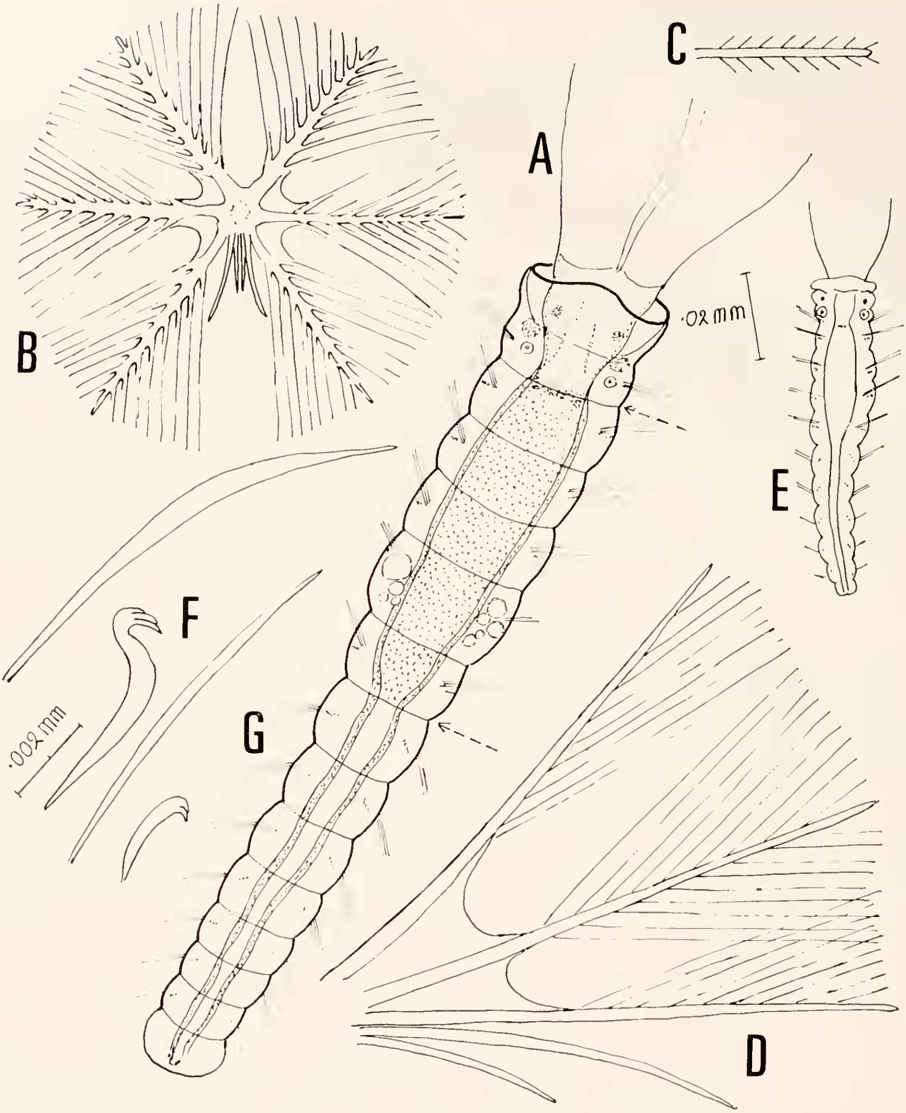

FIGURE 1. General structure of an interstitial sabellid species: A, full grown female individual at onset of sexual maturity; gonads, male or female, develop only in the last but one thoracic segment; B, crown of tentacles seen from anterior end, showing three pinnule-bearing radioles together with two simple tentacles on each side, and mouth at center; C, a pinnule bearing stiff hairs; D, side view of a lateral tentacular complex with the three tentacular radioles bearing long pinnules, a web uniting the basal part of the radioles, and the pair of abortive, explorative tentacles; E, a juvenile, to same scale as in A; F, seta and long-handled hook typical of thoracic segments; and G, seta and hook of abdominal segments.

The pinnules are ciliated and draw water through the external side of the crown and forward through the crown opening, while radiolar cilia cause trapped, microscopic particles to move basally toward the ciliated entrance to the mouth, as in *Sabella pavonina* (Nicol, 1930). Ciliary activity is evident when the crown is expanded but ceases when the radioles close together, *i.e.*, when the worm withdraws into its tube or is actively travelling backward outside the tube. The pinnules also bear stiff pointed hairs (Fig. 1C) which appear to be offensive but not toxic to the larger ciliates coming in contact with them. In addition to the tentacular complex just described, two additional radioles on each side, lacking pinnules and relatively small, serve as explorative tentacles when the worm is free of its tube and moving forward (Fig. 1B, D).

The base of the crown on each side exhibits a groove (Figs. 1A, 2A), which in larger species indicates the line of autotomy, allowing sacrifice of the crown and survival of the remainder of the individual when pulled by a predator. In the present species such a hazard may not exist, and the autotomy groove may be a relict persisting in spite of an extreme degree of dwarfism.

The collar segment, next to the prostomial, tentacular crown, is comparatively simple, the collar rim being undivided, not developed into folds, as in most sabellids. In larger forms the collar is mainly responsible for adding detrital and other materials to the growing distal end of the mucous tube. In this species the collar and related features are so small, relative to the size of the particles available for tube reinforcement, that such collar activity is not feasible. Detritus particles, however, do adhere to the sticky external surface of the delicate mucous tube throughout its length.

The tube of mucus, open at both ends, is quickly formed wherever and whenever the individual comes to rest. While the crown is generally protruded anteriorly for feeding and respiration, the worm periodically withdraws completely and can reverse its position within the tube in spite of close confinement. Any disturbance, however, and any direct exposure to a source of light, causes the worm to wriggle backward from the tube and to progress in a straight line, leaving a trail of mucus behind it. As it does so, it intermittently sweeps the posterior half of its body through nearly 180 degrees in an exploratory manner, an activity that persists until contact with dense detritus and comparative shade is encountered. Action then ceases, a new tube is formed within a few minutes, the crown is protruded, and ciliary currents are re-established. The animal may also advance forward, at which time the pair of simple radiole tentacles on each side explore any substrate within reach.

In a number of sabellid species the posterior terminal structure, the pygidium, bears a pair or several eyespots, particularly among the smaller species of the Fabricinae (*e.g.*, *Fabricia sabella*). The activity just described suggests that pygidial light-sensitivity exists even in the absence of such visible ocelli. Pigment in the present species is restricted to the pair of larval eyes persisting in the cerebral ganglia of sabellids (Wilson, 1936; Downer, 1961), none being present on the body or tentacles. The relative transparency, however, exposes the cephalic ocelli to light even in fully mature individuals, whereas in large individuals of other species, tissue density tends to obscure the ocelli.

A pair of otocysts (Figs. 1A; 2A, C) are distinguishable in life behind the base

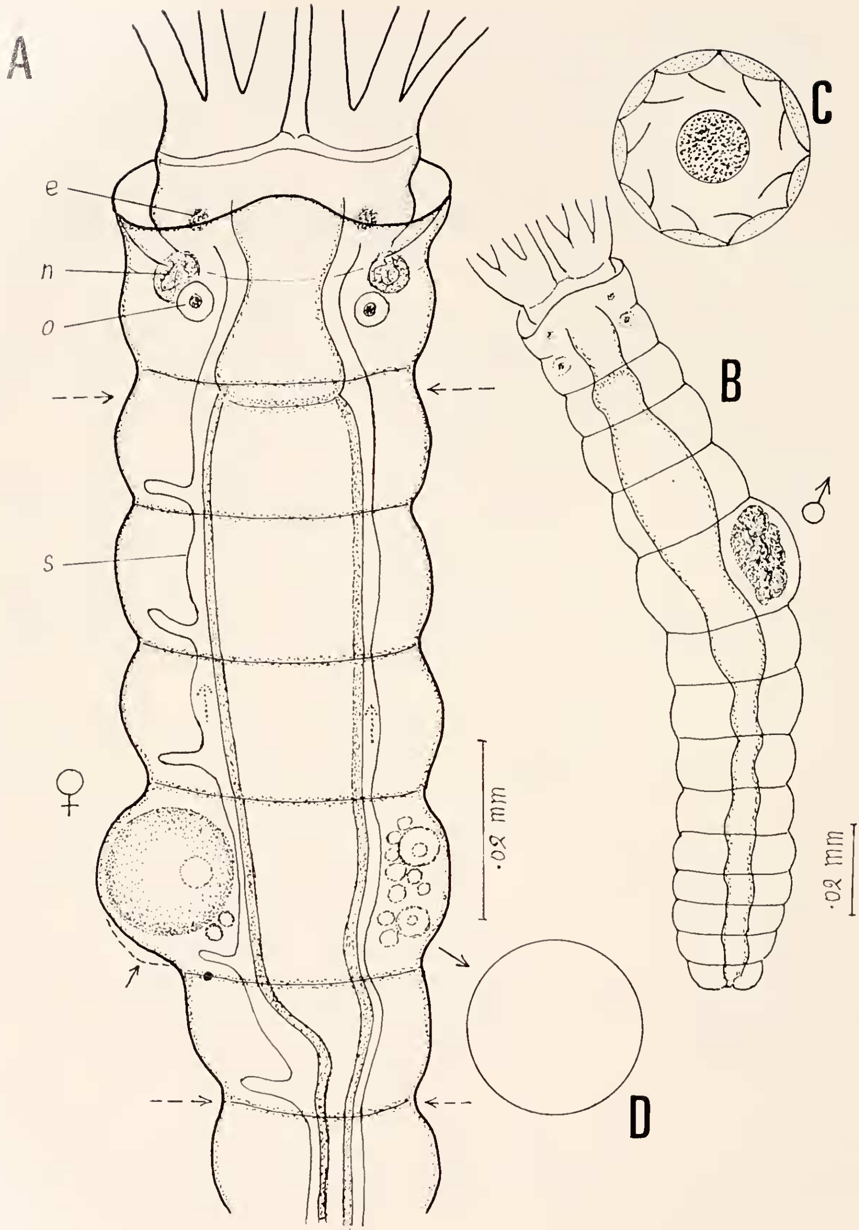

FIGURE 2. Male and female individuals seen from ventral side (not to same scale), parapodial structure not shown. A illustrates the thorax and head region of a mature female, the head showing prostomial ocelli, collar, and "prethoracic" setigerous segment with otocysts and nephridia; the junction between the oesophagus and thoracic stomach is indicated by the distal broken arrows, the junction between thoracic gut and abdominal intestine by the

of the collar, in the first setigerous segment. Each otocyst consists of a closed vesicle containing a birefringent granule and is formed by flattened epithelial cells, about eight in optical section, each bearing a long cilium or flagellum. The granule exhibits a barely discernible movement.

Internal organization and activity

A pair of nephridia, located very close to the otocysts, brownish in life, open anteriorly into the trough formed by the collar with the prostomial crown (Fig. 2A). In most sabellids this pair of nephridia extends posteriorly throughout the thoracic segments. Here, they remain restricted to the first such segment, as in serpulid polychaetes.

The form and subdivisions of the gut are readily seen in the living state. Three regions are clearly distinguishable, namely, prothoracic, thoracic and abdominal (Fig. 2A). The prothoracic, or oesophageal region extends from the mouth to the posterior limit of the first setigerous segment. At the junction with the thoracic gut, a dark narrow transverse heavily-ciliated band indicates a sharp transition from the light brown thin-walled oesophagus to the dark brown thicker wall of the thoracic region or stomach (Fig. 2A). The stomach extends posteriorly to the limit of the thoracic segments, *i.e.*, to the thorax-abdominal junction, indicated externally by the parapodial dorso-ventral inversion, where it changes sharply to a relatively narrow intestine extending to the pygidium. This conformity of internal, gut differentiation with external, body wall differentiation holds for both juvenile individuals which have four fully thoracic segments and for mature individuals which have five (segments with both setae and hooks, and excluding the first setigerous segment which has setae but no hooks).

The conversion of a four-thoracic segment juvenile to a five-thoracic segment adult involves the external body wall (epidermis) and the gut to the same extent. One complete segment transforms from abdominal to thoracic type (Fig. 1A, E), with dorsal setae and ventral hooks replacing dorsal hooks and ventral setae.

Most of the gut is enclosed by a vascular sinus containing greenish (choloro-cruorin) blood (Fig. 2A). Regular peristaltic waves in the sinus wall commence at the posterior end, in the first prepygidial segment, and move anteriorly to the junction of stomach and oesophagus, where they cease. Blood flows steadily and continuously forward through the sinus to the prothoracic nephridia and the peristomial structures, but is not actively propelled by the prothoracic segments. There are no branchial hearts. Notably, in the thoracic segments proper, but not in the abdomen, a blind lateral diverticulum extends from the sinus in each segment, on the right side only (Fig. 2A). These almost certainly correspond to the paired lateral blind vessels typical of other sabellid polychaetes. It is of interest that when the first abdominal segment transforms to bcome the fifth thoracic segment, a typical diverticulum develops in that segment (Fig. 2A).

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lower broken arrows. The whole thoracic gut is enveloped by a vascular sinus with blind lateral branches on the right side (left side of drawing), the dotted arrows showing direction of waves. Oocytes form only in the fourth thoracic segment and mature singly, alternatingly one on each side. B shows mature male with testis on right side only; C, enlarged drawing of otocyst; and D, ripe egg at same scale as A, immediately after being extruded from the fourth thoracic segment.

Individuals become sexually mature following the conversion of the first abdominal segment to become the fifth thoracic. Gonads develop only in the fourth thoracic segment (Figs. 1A, 2A). Sexes are separate. An ovary develops on each side when the abdominal region of the worm consists of about seven segments, the usual maximum number in females. The mature ovum is approximately 140 microns in diameter, which may be more than half the entire width of the worm. Only one ovum at a time grows to maturity, apparently alternating in one side and the other. It escapes by rupture (possibly pore expansion) of the posterolateral segmental body wall of the respective side (Fig. 2A). The next largest oocyte is seen on the opposite side. Altogether as many as nine oocytes have been seen in squashed individuals. Simultaneous full growth of more than one oocyte would inevitably be too destructive to adjoining structures and probably to the whole organism. In male individuals a testis develops only on the right side of the fourth thoracic segment (Fig. 2B), in individuals with at least seven abdominal segments. As many as nine abdominal segments have been seen in male individuals.

Discussion

The marine interstitial habitat is typical for newly settled larvae of diverse kinds, usually following larval metamorphosis. The survival of such minute organisms in an environment of unstable sand grains or detritus is commonly an essential prelude to further growth and subsequent reproduction. Whether the final state is mobile or sedentary, and however large or small, an initial explorative phase is common during postlarval development. Postlarval organisms may accordingly make this their permanent way of life on two conditions, namely, that they do not grow beyond a critical size relative to that of the environmental particles and that they attain sexual maturity. The species described here meets both conditions.

To begin with, juvenile features are retained into the adult state. This is most evident in the number of thoracic and abdominal segments produced, in the number and nature of the tentacles comprising the prostomial crown, and in the abortive and one-sided development of the segmental blood vessels. Thoracic segments are initially four and through abdominal transformation increase to five, whereas the number of thoracic segments typical of the family is seven or eight, irrespective of the number originally present in the postlarval stage. Tentacular radioles are restricted to five on each side, two of which remain small and without filaments, which is a transient phase of growth for members of all larger species. Gonads, male or female, respectively, develop only in a single specific throacic segment. Prepygidial addition of new abdominal segments merely increases the number from the five originally present in the newly settled individual to less than twice that number. Everything indicates a cessation of growth at the equivalent of a very early juvenile stage.

The growth and release of a single egg, one at a time, is obviously the absolute minimum for sexual reproduction, and is an invariable characterstic of this species. Two questions arise. Could smaller eggs, permitting smaller body sizes for sexually mature individuals, serve the developmental or adaptive needs of the species? The answer is conditional. The eggs of many polychaetes are small, with little yolk, with a diameter within 60 to 80 microns (Marsden, 1960; Shearer, 1911). Such eggs develop typically with trochophore larvae, with a feeding planktonic phase before settling. This is true of those species of serpulids so far known, a group which is united with sabellids to comprise the Sabelliformia. Conceivably, therefore, sabellids could persist even if their eggs were of the same small dimensions. Eggs of sabellids, however, are, without exception, so far as is known, considerably more yolky and have a diameter ranging from about 140 to more than 200 microns, which not only results in a comparatively larger size at the time of settling but also obviates both the need and even the capacity to feed before doing so. This interstitial species, therefore, can be said to represent the extreme condition of dwarfism possible for a sabellid species without involving a radical change in developmental procedure.

Gonads first appear and grow only when body growth as a whole is complete. Growth of the one seems incompatible with that of the other, which could mean merely that, once gonad development has been initiated, virtually all nutrition is diverted to gonadal growth. Whatever truth may lie in this explanation, however, it is not the whole answer. Gonads may form because growth generally has ceased, or general growth may cease because gonads are differentiating but not necessarily as the result of nutritional competition (Berrill, 1961). In any case a question remains. Why do new segments fail to appear in the prepygidial growth zone even in their initial minute form, or, alternatively, why is sexual maturity so precocious? In relation to the latter, what little is known concerning polychaete neurohormones indicates that their effect is to inhibit, rather than stimulate, the onset of sexual maturity (Golding, 1968). The major problems therefore remain, namely, what determines the limits of organismal growth and in what way does the attainment of sexual maturity relate to this? An entirely comparable phenomenon is seen in ascidians, where interstitial polycarpid and molgulid species of this typically sessile group have become minute and even motile (Monniot, 1965), and are sexually mature when about two millimeters long, with gonads producing only a few eggs only although these are of normal size.

Summary

The anatomy and behavior of a species of the sabellid polychaete subfamily Fabricinae, is described. Mature individuals are virtually microscopic and represent the extreme degree of dwarfism apparently possible for a sabellid. Eggs are matured and liberated unilaterally, one at a time, from a single thoracic segment. Dwarfism in this species is essentially a cessation of body growth at a juvenile stage, accompanied by precocious sexual maturity, as an adaptation to persistent occupation of an interstitial detrital habitat.

LITERATURE CITED

Berrill, N. J., 1961. Pages 199–208 in *Growth, development and pattern*. Freeman, San Francisco.

Downer, P. J., 1961. The central nervous system and eye spots of sabellid polychaete worms. *Thesis, McGill University*, Canada, 179 pp.

Golding, D. W., 1968. Endocrinology, regeneration and maturation in *Nereis*. *Biol. Bull.*, **133**: 567–577.

Marsden, J. R., 1960. Polychaetous annelids from the shallow waters around Barbados and other islands of the West Indies, with notes on larval forms. *Can. J. Zool.,* **38**: 989–1020.

MONNIOT, F., 1965. Ascidies interstitielles des cotes d'Europe. *Thesis, University,* Paris, France.

NICOL, E. A. T., 1930. Feeding mechanism, formation of tube, and physiology of digestion in *Sabella pavonina. Trans. R. Soc. Edinb.,* **56**: 537–598.

SHEARER, C., 1911. On the development and structure of the trochophore of *Hydroides uncinatus* (Eupomatus). *Q. J. Microsc. Sci.,* **56**: 543–591.

WILSON, D. P., 1936. The development of the sabellid *Branchiomma vesiculosum. Q. J. Microsc. Sci.,* **78**: 543–603.